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H. B. Sifton.

Some Characters of Xylem Tissue
in Cycads.
and
The Bar of Sano and Primordial
Pit in the Gymnosperms.

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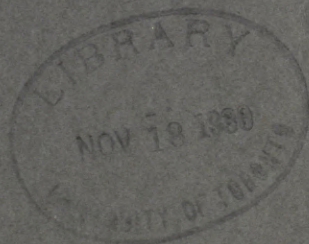
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Some Characters of Xylem Tissue in Cycads

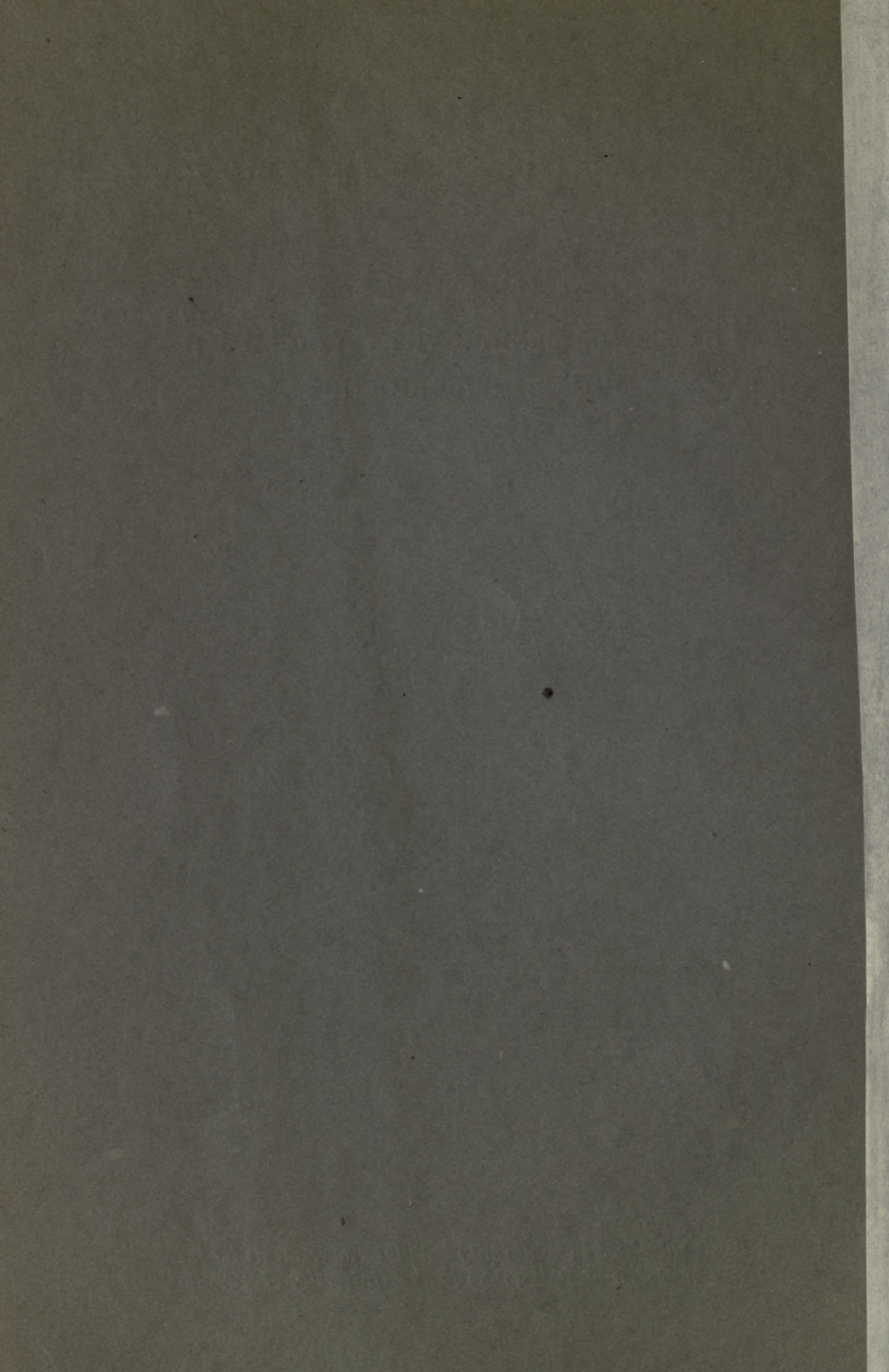
and

The Bar of Sanio and Primordial Pit in the Gymnosperms

old
H. B. SIFTON



*A thesis submitted in conformity with the requirements for the
Degree of Doctor of Philosophy in the University of Toronto*



SOME CHARACTERS OF XYLEM TISSUE IN CYCADS

H. B. SIFTON

(WITH PLATES XXXVII, XXXVIII AND ONE FIGURE)

The detailed investigation of certain anatomical features of the Cycads has been undertaken in the hope of throwing light on the origin of the more specialized structures occurring in the higher Gymnosperms. In recent years considerable work has been devoted to determining the details of anatomical structure in the Conifers. These details have been given much prominence as evidences of the inter-relationships of the various groups. A lack of knowledge of the ancestry of the structures themselves; however, has minimized their value as criteria in phylogenetic investigations. This knowledge can be supplied only by a study of primitive forms.

Pitting

The shape and arrangement of bordered pits in the woody tissue have long been regarded as valuable phylogenetic data. It is largely owing to these features that the Araucarians have been supposed to be closely related to Cordaitean forms, and many botanists still hold this view, notwithstanding the arguments advanced by JEFFREY (6) and SEWARD (9) in favor of different lines of ancestry for the family. In 1907 GOTHAN (4) worked out a phylogenetic line of development of bordered pitting, considering the most primitive type to be hexagonal and crowded over the whole tracheid wall. According to his theory, the pitting next became eliminated from the tangential walls, but still covered the radial as before. A further elimination resulted first in small isolated groups of pits, then in the uniseriate flattened condition, and finally in the scattered arrangement, where the pits occur singly on the tracheid wall. This series of eliminations took place on the middle part of the wall of the tracheid, the crowded arrangement being retained on the ends to facilitate vertical movement of the sap. GOTHAN found his types of arrangement combined in a fossil plant, but in no living form.

JEFFREY is more conservative than many others in his estimate of the significance of pitting, but considers that it is of distinct value in classification when its character in all parts of the plant is considered. On this ground, in his work on the Araucarineae, he accepts the presence of opposition pitting in the cone axis, and scattered pits in the seedlings, as denoting descent from an Abietineous type. He has neglected the character of the pitting in primitive forms such as the Cycads, however, and his interpretation is not in harmony with the facts which these forms disclose. This was done, notwithstanding the fact that as early as 1840 DON (2) recognized the value in phylogeny of the study of Cycads. He carefully worked over the character of tracheids by such methods as were in vogue at that time, and agreed with MEYENS, a still earlier investigator, that the spiral, scalariform, reticulate, and border-pitted types could be referred to a common origin. The importance of these transitions was emphasized also by PENHALLOW (7) in 1907 as affording valuable data on the ancestral character of the bordered pit of the higher forms. In 1919 BAILEY (1) argued that opposite pitting is formed by the breaking up of bordered scalariforms, and that the alternate type was formed from this by a "staggering" of the rows of pits.

In this paper certain features of the primary wood of the Cycads will be considered first. Fig. 1 is a longitudinal section of the petiole of *Cycas revoluta*, showing the tangential walls of the tracheids in the neighborhood of the protoxylem. The tracheid *a* shows the characteristic spiral and scalariform structure of the protoxylem. In transverse section (not figured) the scalariform bars are seen to arch over the intervening spaces so as to form very narrow borders. On the cell *b* the scalariforms are more closely approximated, and through the slits may be seen shorter pores, belonging to the adjacent wall of the next tracheid. The tracheid *c* also shows this clearly. In the other two tracheids typical bordered pits are present. The type of scalariform from which such bordered pits are formed is shown in fig. 2. It is a scalariform similar to that formerly described, except that the borders are wider. Fig. 3, another section from a *Cycas* petiole, indicates transitions in the formation of ordinary bordered pits from this

type of scalariform. Below the center of the figure is a scalariform reaching from side to side. Its border shows constrictions at two points, evidently the beginning of a division into three bordered pits. In the portions of the tracheid above and below, complete divisions and other incomplete ones are in evidence. The name "fusion pits," which has been applied to similar appearances, is evidently a misnomer in this case. They plainly represent phases in the breaking up of the ancestral scalariform rather than the union of two of the more specialized bordered pits. The small pits on tracheids *a* and *b* of fig. 1 in all probability are formed from the narrow bordered scalariforms in a similar manner.

Figure 4 is a much lower magnification of a longitudinal radial section of the fossil stem of *Lyginodendron Oldhamium*, acknowledged to be one of the most ancient of the seed plants. This form had attained in the secondary wood of its stem the condition represented in GOTHAN'S second type, the pits being practically eliminated from the tangential walls (cf. SCOTT 8), but crowding the radial walls from end to end of the tracheid. Wherever the cell wall is present in the figure it is seen to be completely covered with the type of pitting known as reticulate. A careful examination of the pits shows them to be of the same type as those in fig. 1, which had their origin in the narrow bordered scalariforms.

The stem of *Cordaites* (fig. 5) has pits which, like those of the Cycads, have probably originated from the cutting up of wide bordered scalariforms, a condition quite in keeping with the general higher type of wood structure exhibited in the Cordaites forms.

Further evidence of the origin of the bordered pit from the scalariform is found in the secondary wood of certain of the Cycads. A type of fusion pit which recalls the condition in the narrow bordered scalariforms of fig. 1 is shown in fig. 10, which is a radial section of the stem of *Dioon spinulosum*. The three pits nearest the top are of the short, slightly flattened type quite common in these forms. The next three are more elongated. All show the characteristic cross pores of adjacent elements. The seventh of the series is a pit of the second fusion type. It appears like two pits, each with a short pore, with a common long pore crossing both.

On one tracheid wall (in this case the one beneath) two separate pits have formed, each with its own pore; while on the adjacent wall of the next tracheid, one large, somewhat scalariform pit has been retained. Just below this comes a pair of completely separate pits, from their shape and approximation evidently formed by the division of what potentially was a single long one. Then come two more pits of the fusion type, after which the regular type of pitting is resumed. Such examples are often found at the ends of tracheids, where, as noted later, there are other primitive characters.

The multiseriate condition is the most common arrangement of pits in Cycads. In some cases the pits are so closely approximate as to appear slightly flattened. This is the typical condition in the Cordaiteae as described by SCOTT, and has generally been considered the most primitive bordered condition, although more specialized than the reticulate type. The outline of the pits in the Cycads, however, is more often curved.

In the Cycads the scattered type of pitting is also found, originating by the elimination of pits from portions of the tracheid. Fig. 6 from a radial section of a *Dioon spinulosum* stem shows this feature. In the lower part of the right hand tracheid we have biseriate pitting covering the radial wall, with here and there a pit obliterated. The position of the vanished pits is indicated by lighter areas caused by the thinning of the primary wall. These are the primordial pits of Sanio, which have formed as if bordered pits were to be located over them as usual. Farther toward the top is a single row of somewhat flattened pits, an arrangement common in the Araucarians. Still farther up some of the pits have become smaller, while others have been eliminated entirely, thinning of the primary wall being visible here and there. This scattered pitting is seen also in other tracheids of the figure, the primary pit areas being very evident, especially just above and below the center of the second tracheid from the left. At the center is an interesting small bordered pit surrounded by a slightly larger area, probably the boundary of the primordial pit. This seems like a case of partial elimination. The irregular obliteration of the pits has left in some places isolated groups of pits like those

referred to by GOTHAN. A further eccentricity of the elimination is illustrated in the tracheid to the right of fig. 11. The lighter colored pits have typical bilateral borders, while the obscure ones are unilateral, the corresponding pit on the overlying tracheid not having been formed.

The arrangement of pits, opposite or alternate, deserves notice. In fig. 6 two or three pits occur in a horizontal row. In some cases as many as four such pits have been found. In the more common condition, not figured, the pits are regularly alternate, sometimes round, and sometimes flattened by mutual contact. Just as the scalariforms of one tracheid are horizontal while those of the next are inclined, and either straight or curved and irregular (fig. 1), so on one tracheid is found the opposite arrangement of pits, and adjacent to it the alternate. There seems no reason for believing that alternate pitting is formed by any disarrangement of rows of round bordered pits. More specialized plants have one or other of these types predominating; for example, the alternate and flattened arrangement in *Araucarineae*, and the scattered, grouped, and opposite in the *Abietineae*. The presence of all these conditions in mature Cycad wood, as well as in the ancient fossil form described by GOTHAN, modifies to a great extent their phylogenetic significance in higher forms. It strengthens BAILEY'S statement that the presence of opposite pitting as well as alternate in the cone axes of *Araucarians* cannot properly be used as an argument for their descent from the *Abietineae*, and neither is the same condition in primitive parts of pines an evidence of descent from an *Araucarian* type. It would seem that if these facts have any significance in phylogeny, they indicate that both pines and *Araucarians* are descended from lower forms which contained both these arrangements.

It may be stated in passing that both opposite and alternate arrangements of pitting occur in the *Cordaiteae*, the alternate, however, being greatly predominant. Instances of opposition pitting in *Cordaites* may be seen in fig. 5, in the upper part of the right hand pitted tracheid. There is an example also near the lower end of the second tracheid to the left of it. Instances of GOTHAN'S grouped arrangement are also present, especially in the

lower central part of the figure. The uniseriate and scattered arrangements occur, being formed probably by the suppression of pits, as in the Cycads. The only evidence of this in the fossil section, however, is the decreased size of many of the pits in the region of elimination. A careful examination of fig. 5 will make this point clear.

It will be seen from the foregoing account that the Cycads, besides giving indication of the mode of formation of the bordered pits from the scalariform type, afford valuable data on the interpretation of the arrangement of pits. The elimination in these low

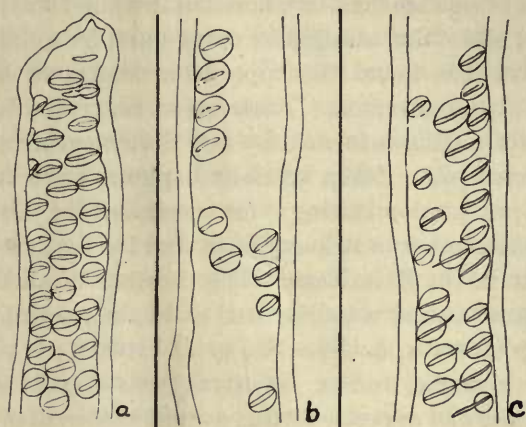


FIG. 1.—*Cycas revoluta*: radial views of different regions of tracheid from stem; *a*, end of tracheid; *b*, normal pitting at contact of two tracheids; *c*, pitting in contact with medullary ray.

forms shows no indication of following a definite law, but proceeds promiscuously, giving rise to all the various types of pitting. It is practically restricted, however, to the middle part of the tracheid, the terminal portions and those parts in contact with the ray cells remaining multiseriate.

The terminal and ray pitting of the tracheids has always remained primitive in another respect. This is indicated in text-fig. 1, which is from a tracheid of the stem of *Cycas revoluta*. In this figure *a* represents the terminal pitting, *b* the ordinary pitting, and *c* the ray pitting of the same tracheid. The pits and their pores are longer in *a* and *c* than in *b*. The pores often extend

beyond the borders in *a* and *c*, and thus recall the condition where pits are forming on scalariform elements (fig. 3). Many of the pores were measured for definite comparison, and the tracheid figured does not exaggerate the difference in pit and pore lengths. Ray pitting on *Dioon spinulosum* secondary stem wood is shown in fig. 9. Here also the multiseriate pitting is present, accompanied by the elongated pore. The left hand tracheid of fig. 11 shows the same type of pore, where a vertical parenchyma cell is in contact with a tracheid. Evidently the primitive type of pore occurs wherever a tracheid is in contact with any type of parenchyma cell. Similar primitive features have been recorded by THOMSON (11) in Araucarian ray pitting.

Tertiary thickenings are common on the tracheid walls, taking the form of spirals or scalariform bars with long shallow pits between. They occur whether bordered pits are present or not, and often traverse the region of the border itself, but have never been observed to cross the pores. PENHALLOW regarded such thickenings as relics of the ancestral manner of deposition of the cell wall, a view which is strengthened by their presence in these low forms.

Bars or rims of Sanio

Considerable importance was attached for some years to the presence or absence of "bars" or "rims" of Sanio. Miss GERRY (3) in 1910 showed them to be present in all families of the Conifers except the Araucarians, and made this a distinguishing feature between both fossil and living Araucarians and other coniferous forms. JEFFREY (6) and THOMSON (11), however, in practically simultaneous publications described bars from the transitional region of the pitting in the cone axis of an Araucarian. This JEFFREY interpreted as evidence of the derivation of Araucarians from the Abietineae. He recognized that this evidence would be invalid if all primitive types of pitting had bars of Sanio, and looked for them in primitive regions of *Cycas* but failed to find them. Their presence here was described later by the writer (10), and invalidates his conclusions. JEFFREY's misstatement has no doubt been responsible for the exaggeration of the importance of

the structure, and probably led to the rejection of all other criteria, making the bar "an infallible test for tribal affinities" (HOLDEN 5), both in fossil and living Conifers.

In 1919 BAILEY (1) studied the origin and development of bars of Sanio, and concluded that those in transition regions are merely normal middle lamellae left between thinned pit areas in the primary wall. He states that when the pits are opposite the bars go smoothly from side to side of the tracheid, because the pits are formed on one primary scalariform pit area, and the bar is the thickening of the lamellae between this area and the next. This theory, however, will not explain the bars figured in the writer's paper of 1915. Those shown in *Araucaria* are connected with pits in regular horizontal rows, but still fork, following round the circumference of each pit, so as to leave clear diamond-shaped areas bounded by opposing forks. These small areas cannot be considered to be other primary pits. The same fact holds for the bars in the *Cycas* petiole, which fork, and are even split into two separate rims in some cases, although the pits are not far enough apart to make it possible to attribute the thin space to another primary pit area.

Bars of Sanio have now been found in other portions of Cycads than the transitional primary xylem. Figs. 6 and 7 illustrate them in the stem wood of *Dioon spinulosum*. These bars often extend beyond the margins of the pits with which they are in contact, as in the middle tracheid of fig. 7 near the bottom, and so are of a higher type than those figured in the former paper. They are still much more primitive than those of the Abietineae, however, lying in close contact with the pits, whenever such are present. Fig. 6 shows the ordinary type of bar in this plant. Between the pits of the single row on the right are bars of the regular Araucarian type. Their length is not greater than the borders to which they cling, and they spread slightly at the ends. The pitting of this tracheid is conspicuously of the opposite type, so that if BAILEY'S theory of the origin of the bars is entirely correct, they should in this case pass beyond the pits to the limit of the tracheids. In the two left-hand tracheids of fig. 6 is shown a condition which is quite common, namely, the presence of these bars in connection

with primordial pits from which the secondary pitting has been eliminated.

Trabeculae

These spool-shaped bars, extending in radial series across the lumens of adjacent tracheids, have received considerable notice in literature, owing to the confusion which arose in some cases between them and bars of Sanio. They have not before been figured in the Cycads, but are present, as shown in fig. 8, a radial section of *Dioon spinulosum* stem. They contain a core or axis composed of a substance which stains in the same way as the middle lamella of the cell. This core pierces the tangential secondary walls of the tracheid and joins up with the middle lamella. These structures are present in higher forms, but their significance is not known. Since they connect with the primary wall, they must have been laid down before the beginning of secondary thickening.

Summary

1. A study of the primary and secondary wood of Cycads indicates the development of reticulate, alternate, and opposite pitting directly from scalariform types.

2. The grouped, uniseriate, and scattered pitting characteristic of higher forms is shown to be formed by the elimination of pits. In low forms, of which the Cycads are a type, this elimination proceeded without apparent order, forming all types of grouping indiscriminately.

3. Similar arrangements of pits occur in Cordaites, although its type has become more fixed than is the case in the Cycads.

4. The Cycads, like the Araucarians, have more primitive types of pitting at the ends of tracheids and where they come in contact with parenchyma.

5. The xylem of certain of the Cycads quite commonly exhibits spiral tertiary thickenings.

6. Bars of Sanio of the Araucarian type are found in both primary and secondary Cycad wood. An elongated type of bar is also present. The Araucarian type is considered the most primitive in living seed plants. No explanation of its origin is offered by BAILEY's theory.

7. Trabeculae are present.

This work was done with the advice of Professor R. B. THOMSON. I am indebted to him, not only for advice and encouragement, but also for the supply of materials necessary for the work.

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DESCRIPTION OF PLATES XXXVII, XXXVIII

PLATE XXXVII

FIG. 1.—*Cycas revoluta*: petiole; tangential section of primary wood; $\times 225$.

FIG. 2.—*Zamia integrifolia*: petiole; pitting of primary wood; $\times 445$.

FIG. 3.—*Cycas revoluta*: petiole; primary wood, showing transitional pitting; $\times 445$.

FIG. 4.—*Lygenodendron Oldhamium*: radial section of secondary wood of stem; $\times 100$.

FIG. 5.—*Cordaites* sp.: radial section of secondary wood of stem; $\times 225$.

PLATE XXXVIII

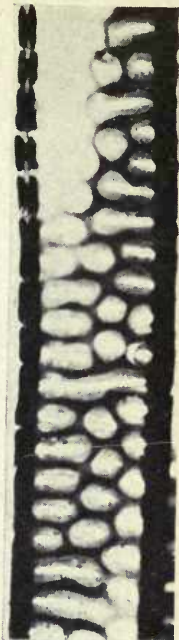
FIG. 6.—*Dioon spinulosum*: radial section of secondary wood of stem. showing pit arrangement and bars of Sanio; $\times 225$.



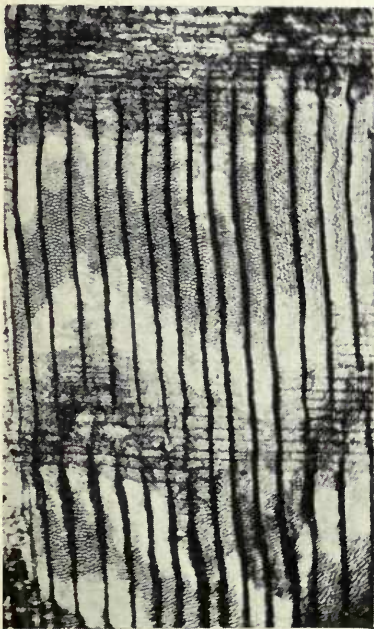
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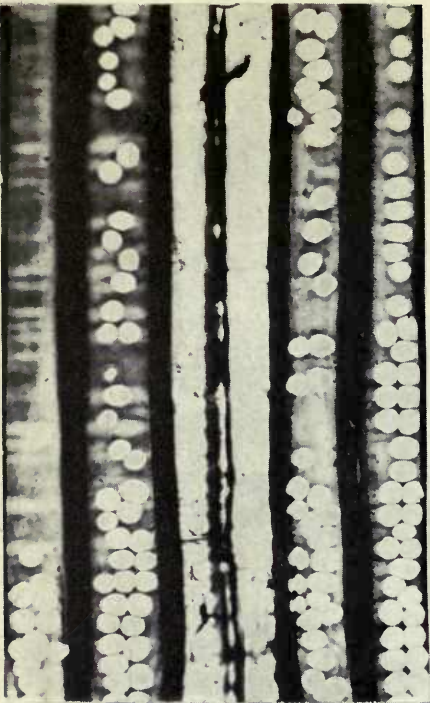
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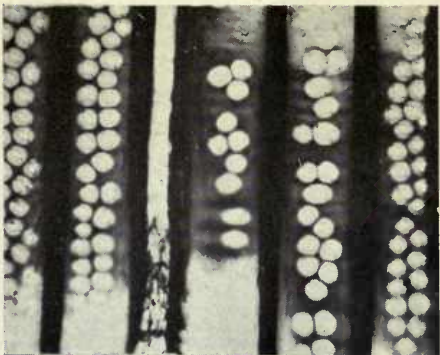
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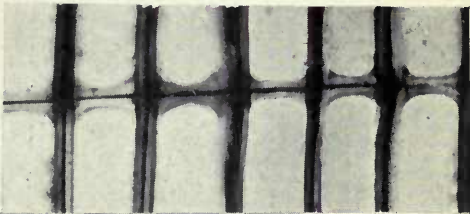
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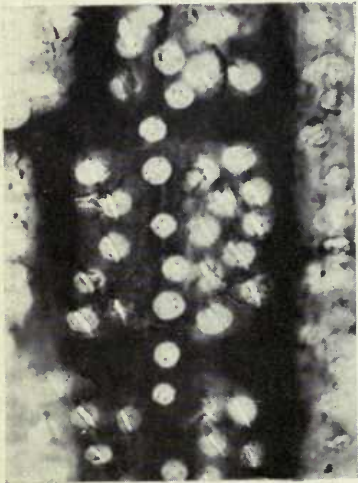
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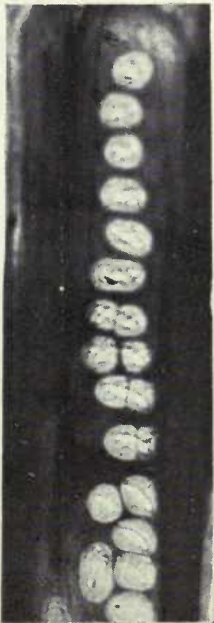
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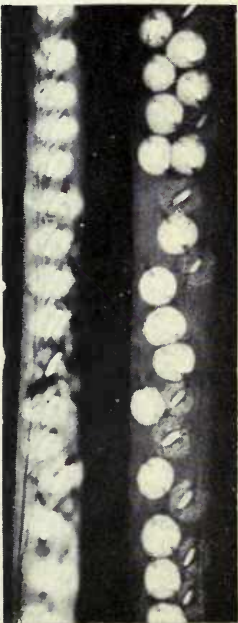
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FIG. 7.—*Dioon spinulosum*: radial section of secondary wood of stem, showing pit arrangement and bars of Sanio; $\times 225$.

FIG. 8.—*Dioon spinulosum*: radial section of secondary wood of stem, showing trabeculae; $\times 225$.

FIG. 9.—*Dioon spinulosum*: radial section of secondary wood of stem, showing pitting in contact with medullary ray; $\times 445$.

FIG. 10.—*Dioon spinulosum*: radial section of secondary wood of stem, with fusion pits near end of tracheid; $\times 445$.

FIG. 11.—*Dioon spinulosum*: radial section of secondary wood of stem, showing pitting in contact with wood parenchyma, and unilateral pits between two tracheids; $\times 445$.

XV. *The Bar of Sanio and Primordial Pit in the Gymnosperms*

By H. B. SIFTON, M.A.

(Read May Meeting, 1922)

Sanio's well-known investigation of the development of the secondary tissues in the Scotch Pine contains the first attempt at critical study of the structures to be considered in this paper. Using material which had been freed of protoplasm by heating with acetic acid, he noted that the cambium cells and the very slightly enlarged cells adjacent to them on the side of the wood are provided with smooth walls of even thickness. Before these wood elements have reached their full size, however, rounded, thin places are observed to form on their walls, and these thin spots enlarge with the growth of the cells. Sanio notes that while horizontally these primordial pits shade off gradually into the thicker portion of the cell wall, the edges above and below are sharply delimited, appearing when mature with "döppelten Umrissen." Since the time of Sanio's publication improved methods of staining have shown that the "double rims" which he observed were merely the edges of a newly developed structure, a thickening in the primary wall of the cell forming a curved ridge above or below the primordial pit. To these ridges the name "Rims of Sanio" has been applied. Where the pits approximate the adjacent rims fuse, taking the form of "Querleisten," the so-called "Bars of Sanio." As seen in tangential section, Sanio refers to these bars as "knotenförmige Verdickungen der Membran zweier Nachbarzellen." On the thinned spaces, or primordial pits, the bordered pits of the secondary wall are formed.

Until the year 1910 very little attention was paid to bars of Sanio, but in that year a paper on their distribution by Miss Gerry (2) aroused a great deal of interest among those engaged in the study of conifers, especially those interested in fossil forms. A paragraph from her conclusions will illustrate the value attached by her to the rims of Sanio:

The distribution of the bars of Sanio above described establishes a constant and useful diagnostic character in the determination of fossil woods. In woods with Abietineous affinities we always find bars of Sanio even though at the same time we may find more or less Araucarian-like pitting. But in the Araucarineae we never find bars, although in fossil forms such as the Araucariopityoideae and the Brachyphylloideae, we find Abietineous as well as Araucarian pitting.

Miss Holden, whose scientific career was unfortunately cut short through the war, made frequent use of Miss Gerry's generalization in her work in fossil botany (4), (5), (6) and (7), considering the presence of bars of Sanio "by far the most reliable criterion for diagnosing coniferous woods."

In 1912 Jeffrey (8) recorded the discovery of bars of Sanio in the secondary wood of the cone axis of four species of *Araucaria*. He notes in his description that each bar does not extend across the tracheid but only across the width of a single pit. The forking where the two rims separate at the ends is also emphasized as one of the indications that the structures are true bars of Sanio. The presence of such bars in a conservative region, like the cone axis, of a form where, as recorded in Miss Gerry's work, it is normally absent, was held by Jeffrey to indicate ancestry from forms which normally had bars of Sanio in their tracheids, and contributed largely to his general conclusions that "the Araucarineae cannot have been derived from the Cordaitales" and "any hypothesis as to the origin of the Coniferales in general must start with the Abietineae as the most primitive tribe." In further support of this theory he states his failure to find bars of Sanio in regions near the primary wood of *Cycas*, *Zamia*, *Ginkgo*, or even *Pinus*. All of these forms, except the last, are by general consent placed among the most primitive living gymnosperms, where Jeffrey's theory also places *Pinus*, although the position of the latter is disputed by other botanists.

Thomson (12) also noted the presence of a bar of Sanio in *Araucarian* wood and considers that it is present in rudimentary form not only in the transitional region of such parts as the cone axis, but in the normal stem wood of all the Araucarineae. He noted that the type of bar in conservative regions of the Abietineae resembles the *Araucarian* bar, while that in more specialized parts differs from it considerably. The suggestion was made that this difference may be connected with an increase in the size of the pitting.

Groom and Rushton (3) made a careful chemical study of the structures in *Pinus Merkusii*, concluding that they are at least partly pectic, and not composed of cellulose as assumed by other writers. After giving an account of their microchemical investigations they say:

Combining the above given facts with Sanio's account of the development of pits in the primary pit-areas the following would, therefore, appear to be the truth. When young the actual marginal portion of the primary pit-area does not thicken by deposits of lignified wall so soon as it does elsewhere (except on the pit-closing membrane) but thickens by successive deposits of pectic substance until a stage is

reached when lignified wall-substance is deposited even over the now thickened rims of the primary pit-areas. Sanio's rims represent a system of rod-like or band-like pectic thickenings of the middle lamella running transversely in the radial walls and linked here and there by slightly curved, longitudinal, band-like, similar thickenings (representing the lateral margins of primary pit-areas).

Bailey (1) in 1919 published the results of researches undertaken with a view to ascertaining the origin of the rims. He suggests the identity of the bars of Sanio seen in *Araucaria* with the normal bands of primary wall situated between the scalariform primordial pits in ferns, and believes that rims and bars in other genera of the conifers and in other groups as well are of the same character. His hypothesis is based on the premise that when a scalariform gives place to a row of shorter bordered pits the primordial scalariform is not similarly cut up. He observes further that in some cases "the elongated bordered pits become replaced by vertical rows of smaller pits which are staggered so that the pits in one row alternate with those of the next series. These pits are usually superimposed over nearly the whole surface of the primary pit areas, and the thicker portions of the middle lamella tend to anastomose or form a reticulum." This, he suggests, accounts for a normal lack of typical bars of Sanio in forms where alternate pitting is strongly developed and makes it difficult to explain how forms with these structures well developed can be descended from ancestors with alternate pitting. In a number of Angiosperms he finds evidence to corroborate his theory, the pits being arranged in long, horizontal rows with bars between, so that the structure of the primary wall is suggestive of that found in lower forms with scalariform bordered pits.

In 1915 the writer (10) discovered bars similar to those previously noted in *Araucaria*, in the petiole of *Cycas*, and later (11) recorded such structures in the secondary wood of *Dioon spinulosum*. Their presence in forms, which are recognized as among the most primitive of living seed plants and which cannot be held to have descended from Abietineae, suggested the correctness of Thomson's idea that this type might be the primitive one from which the Abietineous form originated. It was, therefore, considered worth while to investigate the types of rims or bars throughout the Gymnosperms in the light of this additional knowledge of their occurrence. For convenience of reference certain of the photographs formerly published have been repeated in this paper.

As indicated by the title, the primordial pit of Sanio will be given a considerable amount of attention since rims of Sanio have not been found apart from these thin places in the primary wall.

They are not, however, as Sanio apparently supposed, merely the sloping edges of the hollow.

Fig. 1, Plate I, a portion of a tracheid from the petiole of *Zamia integrifolia*, illustrates the type of broad-bordered scalariform from which the bordered pits of more specialized woods are, from the writer's standpoint, considered to have developed. It will be seen that while in some parts of the tracheid the scalariforms are horizontal, in other parts they are less regular, passing in a diagonal direction across the tracheid. Filling in the space between the diagonal and the horizontally placed scalariforms are the ends of others. The long, slit-like pores reach from end to end of the pits, and the comparatively wide borders can be plainly seen. Between adjacent pits dark lines are shown in the photograph. These appear dark blue in the section, being portions of the primary wall, stained with Haidenhain's haematoxylin. The portion covered by the borders is lighter in colour because the primary wall is thinner in this region. In other words, each scalariform exactly covers a long, narrow primordial pit of the same nature as those described by Sanio in *Pinus*. The strips of primary wall between the pits, where it has retained its normal thickness, are, according to Bailey's view, bars of Sanio.

Fig. 2, Plate I, is a tracheid from the petiole of *Cycas revoluta*. It shows in face view scalariforms which have been cut up to form shorter bordered pits. Near the centre of the figure is one scalariform which persists as a single pit reaching from side to side of the cell, but constrictions can be seen in the border, indicating what might be described as an abortive attempt at division into three. On the rest of the tracheid complete divisions are observed, producing bordered pits which are round, or more or less elongated. It is plainly to be seen that the dark lines extend vertically as well as horizontally between these pits. In other words, each bordered pit has its own separate primordial pit surrounded on all sides by primary wall of normal thickness. This is true though the pits are so arranged that there can be no doubt of the formation of a row of them on what was ancestrally a single scalariform. Even the single scalariform which is left has the thicker primary wall extending into the constrictions on its sides. Sometimes in Cycads one sees a tracheid where the scalariform primordial pit is retained and has a row of bordered pits on it, and this was quite possibly a typical condition in the ancestral forms where multiseriate pitting first originated. The fact that such a habit has largely been lost in forms as low as our living Cycads and that the loss is not dependent on alternation of pitting, is cause for doubt as to Bailey's theory on the origin of the bar of Sanio.

Fig. 3, Plate I, also from a *Cycas* petiole, shows tracheids representing a stage of development beyond that shown in Fig. 2. It will be noticed that the bordered pits are not crowded over the entire surface of the tracheids as in the former figure. In the upper part of the tracheid at the right several bordered pits are plainly missing. The primordial pits remain and are shown as lighter areas surrounded on all sides by dark lines where the middle lamella has not become thinned. Primordial pits on which bordered pits are not superimposed appear darker in the photograph than the others, owing to the fact that the total thickness of the secondary wall covers them. Similar areas, though with the primordial pits less sharply outlined, are present in other parts of the section. Another important development is also present. Above and below certain of the pits the middle lamella is thicker than at their sides, a fact indicated by the deeper staining. This is true not only where opposite pitting is in evidence, but in cases where the pits are alternate and where, if Bailey's theory is correct, the thick part should form a reticulum enmeshing the pits. Several points suggest very strongly that this is an extra thickening of the membrane at the edge of the primordial pit and not merely the normal, unthinned middle lamella. Thus in the left hand tracheid of the figure there are to be seen thickenings in the form of arcs closely applied to the edges of the bordered pits. I have not applied microchemical tests to ascertain whether these arcs are of pure cellulose or of a pectic nature as Groom and Rushton found them to be in *Pinus Merkusii*, but their form and position leave no room for doubt that they are true rims of Sanio. Where the pits are closely approximated the two adjacent rims fuse forming Sanio's "Querleisten." These structures, as in a former paper (10), will be referred to as "bars" of Sanio. In one or two cases, where the pits are not crowded, the rims are separate from each other, e.g., between the second and third pits above the pair of opposite ones.

Fig. 4, Plate I, shows the same structures in the cone axis of *Araucaria Bidwilli*, where they were discovered independently by Jeffrey and by Thomson. In two tracheids of this figure the pitting is opposite, and if Bailey's theory of the bar were correct the structures should extend in unbroken lines from side to side of the tracheid. This, however, is not the case. Each pit has a rim clinging to its edge with the result that small diamond-shaped areas of a lighter colour can be seen between the pits.

Fig. 5, Plate I, illustrates bars of Sanio as seen in a radial section of the stem of *Dioon spinulosum*. The pitting is more or less scattered owing to the elimination of certain of the bordered pits. On the

upper part of the right-hand tracheid are seen bars which, unlike those in Figs. 3 and 4, pass beyond the area covered by the bordered pit with which they are in contact. Their mode of origin is indicated by the bar just above the three grouped pits at the bottom of the figure on the same tracheid. The constriction in this bar shows it to be formed by an imperfect fusion end to end between two short bars, one connected with the bordered pit and the other with an adjacent primordial pit on which no secondary pit has formed, and which shows a tendency to disappear. On the tracheid to the left are shown several bars, some of which strike the sides of bordered pits, indicating that the primordial pitting is alternate. These are interesting from their pronounced thickness as compared with that of the normal primary wall at the sides of the bordered pits, thus bringing out their nature as superimposed structures.

In many cases bars of exactly the appearance of those noted by Thomson in the stem of *Araucaria* are seen in *Dioon*. Such structures are plainly indicated in Fig. 6, Pl. II, separating the six closely approximated pits in the upper half of the right-hand tracheid. Above this group, where the pitting is more scattered, separate rims are in evidence, closely approximated to the bordered pits. The structures are plentiful in the remaining tracheids of the figure, of which the one to the left is especially to be noted, the upper portion showing bars of *Sanio* in a region from which secondary pits have been entirely eliminated.

The method of elimination of bordered pits to produce the "scattered" condition is illustrated in the central portion of Fig. 6, particularly in the second tracheid from the left. In regions of elimination certain of the pits have become smaller than normal. In carefully stained sections the primordial pits of normal size are to be seen with these small bordered pits in the centre, but their outline is so delicate as contrasted with that of the bordered pit that it is difficult to reproduce in a photograph. The condition has been caught by the camera in one case near the centre of the tracheid under consideration. This is the most primitive living plant in which bordered pits which do not cover the whole area of the corresponding primordial pit have been recorded. Elimination pitting also occurs in the *Cordaiales* and the *Araucarineae*, and is important in that it makes way for the larger pits found in the wood of more specialized forms.

For convenience of presentation the remaining groups are considered in the following order: *Cupressineae*, *Taxodineae*, *Abietineae*, *Taxaceae*, *Gnetaceae* and *Ginkgoaceae*. Needless to say, the arrange-

ment is not to be taken as an indication of supposed phylogenetic relationship. Ginkgo is reserved to the last because it is regarded as a special form due to certain features of arrested development.

Fig. 7, Plate II, a radial section of secondary wood from the root of *Chamaecyparis obtusa* (*Retinospora lycopodioides*) illustrates an advanced condition approaching the most specialized in the higher Gymnosperms. With the elimination of large numbers of the pits, which covered the whole radial surface of the tracheids of the lower Gymnosperms, comes the possibility of enlargement for those that are left. In the form under consideration this enlargement has taken place to a very noticeable extent. The primordial pits, outlined by their rims of Sanio, have here increased to a greater area than have the bordered pits, and the rims of Sanio are thus no longer in contact with the latter. The point with regard to these, however, is that while the bordered pits of the secondary wall have been reduced to a uniseriate condition the same is not true of the primordial pits. In each case the bordered pit appears superficially to be inserted on a simple primordial pit reaching from side to side of the tracheid, but a consideration of the rims of Sanio leads to a different conclusion. At the centre of the second tracheid from the left, for example, the bars are plainly in horizontal pairs with a clear space separating the ends. The primordial pits have enlarged, overlapped and fused horizontally, but the end to end fusion of their rims of Sanio is not yet completed, and the gaps indicate the compound origin of the large primordial pit. The forking ends of the short bars show that each is a true bar of Sanio, composed of two vertically fusing rims. In other parts of the section the fusion of bars is complete. In the second bar from the top of the third tracheid from the left the bars are completely united, while the compound nature of the primordial pit is indicated by the imperfectly fused bars below it. In the stem of *Chamaecyparis* complete fusions of the bars are the rule.

It is generally admitted that the ancestral pitting for this and other conifers is multiseriate, and each of the shorter bars discussed above would thus be formed of two or more which have overlapped and fused. This overlapping accounts for the thickness of the bars in this and higher forms, where it is more pronounced than in forms like the Cycads and Araucarians.

Chamaecyparis is not the only genus of the Cupressineae which indicates the mode of formation of the complex bar of Sanio of the higher forms. In the root of *Thuja*, in regions of biseriate pitting, it is often in evidence. Fig. 8, Plate II, illustrates a fairly common condition in the root of *Thuja occidentalis*. Near the centre of the

second tracheid from the left are shown bars incompletely fused, though the ends are not forked as in the very suggestive example illustrated in Fig. 7. The stem of *Thuja* shows a similar condition in regions, such as the ends of tracheids, where biseriate pitting is in evidence. The typical condition in the stem, however, is illustrated in Fig. 9, Plate II, where the pitting on the rather irregular tracheids is uniseriate and the rims and bars are so perfectly fused together as to give no hint of their compound nature. At the right of the figure is shown a little of the summer wood with its narrow lumina and small pits. The rims of Sanio do not come out clearly in summer wood, owing probably to the heavy lignification, but they may be seen between the second and third pits from the top, to be of the same essential nature as those of the spring wood.

A study of several other members of the Cupressineae revealed no great variation in structure from the points already mentioned. In the root of *Thuja Standishii* indications of incomplete fusion of the rims were found, while in the stem the specialization is apparently complete. Material of *Cupressus Benthami* seedling, and various regions of *Thuja plicata*, *Thuja orientalis*, and five species of *Juniperus* was available and in all of these the development of the compound bar is, as a rule, complete. Doubtless relics of the ancestral characters are present in the most conservative regions of some or all of these forms, but they are less plentiful than in those which have been described more in detail.

There is a fairly general tendency for the bars to appear less strongly marked in stem than in root wood, either through their partial lignification or for some unknown cause. They are, however, sufficiently definite to indicate clearly their homology with those illustrated in the stem of *Thuja* (Fig. 9). Even where, as in some species of *Juniperus* (e.g., *J. communis*, *J. davurica* and *J. occidentalis* stems) they have become shortened, it is quite apparent, even without the evidence furnished by the roots, that they border enlarged primordial pits such as have been described.

Passing to the Taxodineae, evidence of the development from the Cycadean-Aruacarian type of primordial pit and rim of Sanio to the more specialized form is again found. Fig. 10, Plate III, is a radial section of the root of *Taxodium distichum*. The pitting here is less scattered but there is evidence of a considerable amount of elimination. In the two middle tracheids there has been a reduction at least from the triseriate to the biseriate condition and the bordered pits have not enlarged sufficiently to fill the space left by the central row which was eliminated. There has not been room for the pri-

mordial pits to enlarge to a great extent vertically but they have done so in a horizontal direction, and fused to form long, narrow pits bordered above and below by straight bars of Sanio passing from side to side of the tracheid. That these bars are compound structures is shown in some cases by constrictions which divide them into three parts corresponding to the ancestrally triseriate primordial pitting. This condition is marked in the seventh bar from the bottom of the second tracheid from the right and in the sixth from the bottom of the tracheid to the left of this. It is to be seen also in others. In this triseriate condition it is remarkable that divisions between the bars, crowded end to end as they are, should be evident even to the degree shown. The divisions are delicate and difficult to photograph, but can be clearly seen in the section.

As shown in the photograph, uniseriate bordered pits are also found in the root of *Taxodium*, though to a less extent than in the stem, which is illustrated in Fig. 14. The bordered pits are larger in proportion to the width of the tracheid, but not large enough to fill the compound primordial pits, which are bounded above and below by well marked rims whose components have become perfectly fused.

In other members of the *Taxodineae* which were available for study the pits even in the roots are more reduced in number, there being a tendency toward the uniseriate condition. In these the bordered pits are inserted typically in broad primordial pits which they do not completely cover, but whose rims have lost any indication of their compound nature. The ancestral condition is indicated in very conservative regions by the presence of bordered pits completely covering the primordial pits and with rims of Sanio closely attached to their borders. This condition will be again referred to when the *Abietineae* are considered. It has been observed in the seedling root of *Cunninghamia sinensis*, and in the root of *Sciadopitys verticillata* near the primary wood.

Fig. 11, Plate III, is a radial section of the stem of *Abies amabilis* and illustrates typical *Abietinean* pitting. The bordered pits are large as compared to those of the *Cycads* and *Araucarians*, and are placed in primordial pits which are still larger, resembling in every respect those whose development has been traced in the *Cupressineae* and the *Taxodineae*. The rims of Sanio do not normally touch the borders except where the pitting is somewhat crowded and even here they pass beyond the individual bordered pit horizontally. In other words, the primordial pits to which the rims attach themselves have increased greatly in height wherever there is room, and even where

crowded they are broad, usually reaching across the face of the tracheid.

That these large primordial pits have originated in the same way as those of the families considered above is proved by a consideration of conservative regions. Fig. 12, Plate II, shows a tracheid from the root of *Pinus strobus* close to the primary wood. The pits are uniseriate, scattered and enlarged, but well marked rims of Sanio are to be seen clinging closely to their borders. In this primitive region the ancestral condition where the size of the primordial pit has not increased beyond that of the bordered pit is retained. Jeffrey (8) apparently overlooked the rims of Sanio in this region, for he states that in *Pinus* "bars of Sanio make their appearance late, and not in proximity to the primary wood," a statement which might be considered correct had Jeffrey made the distinction between bars and rims of Sanio. This, however, he did not do.

A recapitulation of the development of the large, compound primordial pit from the primitive type shown in this figure is exhibited as one passes from the primary wood outward in the roots of various Abietineae. Indications of the fusing of rims end to end occur in a figure of *Larix americana* root by Thomson (12), and have been observed by the writer in the root of *Pinus Lambertiana* and *Pinus strobus*. As one passes out from the centre of the root the primordial pits become larger until the maximum size is reached and the pits and rims have fused to produce a condition such as that illustrated in Fig. 11.

The primitive rim of Sanio is to be seen in other parts of the Abietineae than the roots. In Fig. 13, Plate III, it is present in a radial section of the secondary wood of the cone of *Pinus resinosa* close to the primary xylem. The photograph is poor owing to the irregularity of the tracheids in the region, but rims of Sanio are in evidence in close contact with several of the bordered pits.

In the adult wood throughout the Abietineae, minor variations in primordial pitting are present, though the general type illustrated in Fig. 11 is preserved. In the *Cedrus* stem the rims were sometimes closely applied to the pits. This was observed in wounded material, and the wounds may account for the primitive character. Near the pith, in this form, the same tendency was observed. The nine species of *Pinus* investigated all showed the typical specialized form of rim though with variations in staining properties.

In the Taxaceae the rims of Sanio show evidence of the close relationship of the family to the Pinaceae, for it is evident that the same process of evolution has been followed. In young *Dacrydium*

seedlings the rims are closely approximated to the bordered pits in true Araucarian fashion while in the adult stem they have drawn away and are often much elongated. The same adult structure is found in *Podocarpus*, *Saxagothaea*, *Phyllocladus*, *Torreya* and *Taxus*. A further tendency in the evolution of the primordial pit is illustrated in the family, however, and it is important because it apparently leads up to the Gnetales and lower Dicotyledonous types. The vertical height of the enlarged primordial pit lessens so that while it still reaches from side to side of the radial wall of the tracheid, its edges approach those of the bordered pit above and below. Fig. 15, Plate IV, is a radial section of the root of *Torreya nucifera* where this development has not yet been consummated. Tertiary thickenings, characteristic of the Taxineae, are present, but the primordial pits and rims of Sanio are of the Abietinean type. Fig. 19, Plate IV, is a radial section of the stem of *Taxus cuspidata*, where the tertiary thickenings are still more in evidence. The rims and bars of Sanio are faint but may be made out quite clearly in several of the tracheids. In the Pinaceae such primordial pitting has been noted in regions where the elimination of bordered pits has not gone far enough to permit of vertical expansion, but here it is seen even where the pits are separated, for example, near the centre of the third tracheid from the left, and the condition in primitive Taxaceae, as well as in the more primitive parts of the Taxineae themselves (e.g., the root of *Torreya*, Fig. 15), suggests that it is a further modification of the specialized compound primordial pit.

Fig. 17, Plate IV, is a radial section of the stem of *Gnetum scandens* showing a part of the wall of one of the enormous vessels characteristic of this vine-like form. Between the rows of pits are particularly heavy bars of Sanio outlining long, primordial pits which suggest those of the lower Angiosperms. Their vertical height is very small when compared with the width of a complete vessel, so that, as in the Dicotyledonous form, they at once suggest the primordial scalariforms of Fig. 1, Plate I. A consideration of the wood of other members of the Gentales, and of conservative regions of *Gnetum scandens* itself suggests a different origin.

Fig. 18, Plate IV, is a radial section of the stem of *Ephedra gerardiana*, where the vessels are not so large. Rims of Sanio are not strongly marked but are quite evident, especially in the element to the right. They and the primordial pits enclosed are similar to those of *Taxus*, and there is nothing to suggest a different origin.

Were no further evidence at hand it could scarcely be considered probable that the rims of Sanio in *Gnetum* are simply relics of the

ancestral scalariform while those of the closely related *Ephedra* are the outcome of the series of developments outlined in this paper. Fig. 16, Plate IV, however, shows the *Taxus* type of rim in *Gnetum scandens* itself, in the primary wood. At the left of the figure is a scalariform tracheid, indicating proximity to the protoxylem. The right-hand tracheid belongs to the metaxylem and in it the structures referred to come out clearly between the bordered pits. In general, the phylogenetic development of the metaxylem in a group of plants follows along the same lines as that of the secondary wood, but is less advanced, and in other families of the Gymnosperms where a rim of Sanio has been observed in this region, it is of the Araucarian type. The presence in the primary wood of *Gnetum* of bars such as those illustrated is, therefore, further ground for assuming that the long, well marked bars on the vessels of the secondary wood are a culmination of the series of developments outlined.

A study of various regions in the Dicotyldeons with reference to the bar of Sanio is beyond the scope of this paper, but from the appearance of the structures and the description of them in anatomical literature there is no reason for assuming their origin to be different from that of those found in the Gnetales.

The Ginkgoaceae, of which *Ginkgo biloba* is the only living species, will now be considered. In this form the pitting is generally described as opposite, with bars of Sanio passing from side to side of the tracheid. It is found on careful examination, however, that the elimination of pitting has not gone so far in this as in higher forms, and so the bordered pits and the primordial ones on which they are formed have enlarged to a less extent than those of such forms as the Abietineae. This can easily be seen by comparing the pitting of *Ginkgo* as shown in Plate IV with that of *Abies amabilis*, which is shown at less than half the magnification in Fig. 11, Plate III. The compound primordial pit and bar of Sanio is thus arrested in this form, in the midst of its development and, as would naturally be expected, incomplete stages are very plentiful.

Fig. 20, Plate V, is from a young stem of *Ginkgo*, near the pith, and typical Araucarian pitting is shown. In the left hand tracheid the pits are alternate and flattened to hexagonals by mutual contact—a condition typical of the stem in the Araucarineae. This flattening of the borders is apparently not a primitive condition for the forms in which it is plentiful for it is not characteristic of the most primitive regions of such forms as the Araucarians. In such places the pits are rounded, and separated by appreciable bands of the cell wall (see Fig. 4, Plate I). The crowding is due, apparently, to the general

tendency toward enlargement of pitting even in forms where elimination has taken place to a slight extent or not at all. In the right hand tracheid of Fig. 20 the pits are more scattered, and retain their rounded contours. The only bars or rims of Sanio in the figure are of the short, narrow type found in the Araucarian stem.

Fig. 21, Plate V, is from the short shoot of Ginkgo. Medullary ray cells at the upper right indicate that in the right half of the figure we are dealing with secondary wood, but the pitting at the left is that of the metaxylem. The three right hand tracheids have alternate pitting. The pits are not flattened by mutual contact, and above and below them are bars of Sanio of the type seen in the cone axis of *Araucaria* (Fig. 4, Plate I). The forking at the ends is plain, especially in the third tracheid from the right.

Fig. 22, Plate V, shows the ends of two stem tracheids, and is included because it illustrates a stage often found in Ginkgo. The two pits at the bottom of the right hand tracheid have what appears on casual view to be a straight bar of Sanio between them, but close examination shows two separate rims with ends overlapping but not fused, each rim being connected with its own pit. The rest of the figure has the compound bars rather well fused.

Fig. 23, Plate V, which is from the root, presents a special form of rim resembling that of higher forms more closely than the usual Ginkgo type. There has here been a considerable enlargement of the primordial pits and the rims are curved, and more heavily marked than usual. In parts where the pitting is somewhat crowded, however, their compound origin is still in evidence. See, for example, the thinning out at the centre of the second and third bars from the bottom, and the diamond-shaped, clear area in that fifth from the bottom. Fig. 24 shows bars similarly thinned out at the centre although here the pitting is uniseriate and the thinned place comes opposite the bordered pit. Thus it cannot be said that the gaps are due to a tendency of scalariform bars to break up and adhere to the bordered pits. In the light of the evidence from primitive regions and primitive forms, their presence is easily explained as a relic of the condition in which short bars, each composed of the rims of two vertically adjacent, small primordial pits, were arranged in a series, end to end, across the tracheid.

The three remaining figures illustrate common types of bar in Ginkgo. Fig. 25 is from the same region as Fig. 20, and here the short bars have fused end to end, though the enlargement of primordial pits

in comparison to the size* of the tracheid is small. Under these conditions the bars naturally present a condition closely resembling that found in the stem of *Dioon spinulosum*. The condition shown in Fig. 26 is very common in adult wood—the pits uniseriate and rather close to each other but with clear-cut bars between. In Fig. 27 the secondary pitting has been almost completely eliminated, but the bars are left.

It is thus quite apparent that, owing to the partially arrested development of the primary wall at a stage midway between the Cycadean-Araucarian structure and that found in higher forms, the species is peculiarly rich in evidence bearing on the development of the compound rim and bar of Sanio. A complete series of developmental stages is easily obtained from the one plant. The Araucarian bar is seen in very conservative regions from which Jeffrey believed that all bars were absent, and stages from this to the advanced Abietinean type are scattered freely through the secondary wood of root and stem. Such a condition is in complete agreement with the line of development outlined in the present article.

SUMMARY

1. A study of primitive forms of pitting indicates that soon after short, bordered pits formed on the ancestral scalariforms, the scalariform primordial pits also gave way to rows of shorter ones.
2. Rims of Sanio are probably not relics of the old, primary scalariforms, but new structures resulting from an extra thickening of the primary wall at the edges of primordial pits.
3. The bars or "Querleisten" of Sanio are formed by vertical fusion between the rims of closely approximated primordial pits.
4. Numbers of the bordered pits which covered the radial walls of tracheids decreased in size and were finally eliminated, after which the remaining pits, both primary and secondary, enlarged.
5. The growth of the secondary bordered pit failed to keep pace with that of the primordial pit, which gave rise to rims of Sanio at some distance from the edges of the borders.
6. In all the higher Gymnosperms the enlargement of primordial pits caused an overlapping and fusion of horizontal rows into single broad ones reaching across the tracheid.

*It should be remembered that, as noted by Sanio, the primordial pit increases in size with the growth of the tracheid. This being so the *absolute* size of the primordial pits is not of great phylogenetic interest, through their enlargement *as compared with the size of the tracheid on which they are placed*, is significant.

7. The compound nature of these broad primordial pits is indicated in conservative regions of several forms by the incomplete horizontal fusion of the bars and rims of Sanio.

8. In specialized woods the rims or bars connected with these fused primordial pits have also completely fused, and probably overlapped to form a heavier bar than in the lower forms.

9. There was a final tendency for the compound primordial pits to become narrowed vertically while retaining their horizontal breadth, which probably led to the condition in the lower Dicotyledons.

10. In Ginkgo, the elimination of pitting and the subsequent enlargement of primordial pits did not proceed so far as in higher forms. As a result this form is particularly rich in indications of the mode of origin of the compound rims and bars of Sanio.

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DESCRIPTION OF PLATES

PLATE I

Fig. 1.—*Zamia integrifolia*, petiole; scalariform pitting on primary wood. $\times 340$.

Fig. 2.—*Cycas revoluta*, petiole; transitional pitting on primary wood. $\times 340$.

Fig. 3.—*Cycas revoluta*, petiole; tangential of primary wood showing bars and rims of Sanio. $\times 340$.

Fig. 4.—*Araucaria Bidwilli*, radial of ovulate cone; secondary wood showing bars of Sanio. $\times 340$.

Fig. 5.—*Dioon spinulosum*, radial of stem; secondary wood showing bars of Sanio. $\times 340$.

PLATE II

Fig. 6.—*Dioon spinulosum*, radial of stem; secondary wood showing bars and rims of Sanio and elimination pitting. $\times 185$.

Fig. 7.—*Chamaecyparis obtusa* (*Retinospora lycopodioides*), radial of root; showing enlarged pitting, both primordial and secondary, and bars of Sanio whose horizontal fusion is incomplete. $\times 340$.

Fig. 8.—*Thuja occidentalis*, radial of root; some bars of Sanio incompletely fused. $\times 340$.

Fig. 9.—*Thuja occidentalis*, radial of stem; pitting mostly uniseriate and bars of Sanio with complete horizontal fusion. $\times 340$.

PLATE III.

Fig. 10.—*Taxodium distichum*, radial of root; less elimination of pitting; some bars of Sanio with constrictions indicating their compound origin. $\times 254$.

Fig. 11.—*Abies amabilis*, radial of stem; Abietinean rims and bars of Sanio. $\times 185$.

Fig. 12.—*Pinus strobus*, radial of root close to primary wood; rims of Sanio of primitive type. $\times 340$.

Fig. 13.—*Pinus resinosa*, axis of ovulate cone, close to primary wood; primitive type of rims of Sanio. $\times 340$.

Fig. 14.—*Taxodium distichum*, radial of stem. $\times 254$.

PLATE IV

Fig. 15.—*Torreya nucifera*, radial of root. $\times 340$.

Fig. 16.—*Gnetum scandens*, radial of stem, through primary wood. $\times 340$.

Fig. 17.—*Gnetum scandens*, stem; radial wall of vessel. $\times 340$.

Fig. 18.—*Ephedra gerardiana*, radial of stem. $\times 340$.

Fig. 19.—*Taxus cuspidata*, radial of stem. $\times 340$.

PLATE V

Fig. 20.—*Ginkgo biloba*, radial of stem, near the pith. $\times 432$.

Fig. 21.—*Ginkgo biloba*, radial of short shoot. $\times 432$.

Fig. 22.—*Ginkgo biloba*, radial of stem. $\times 432$.

Fig. 23.—*Ginkgo biloba*, radial of root. $\times 432$.

Fig. 24.—*Ginkgo biloba*, radial of stem. $\times 432$.

Fig. 25.—*Ginkgo biloba*, radial of stem, near pith. $\times 432$.

Fig. 26.—*Ginkgo biloba*, radial of stem. $\times 432$.

Fig. 27.—*Ginkgo biloba*, radial of stem. $\times 432$.



1.



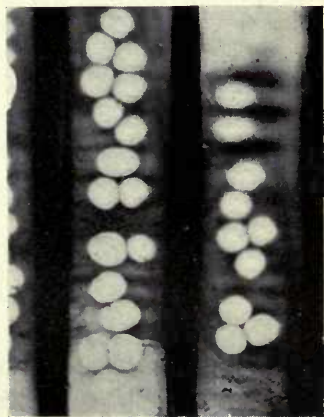
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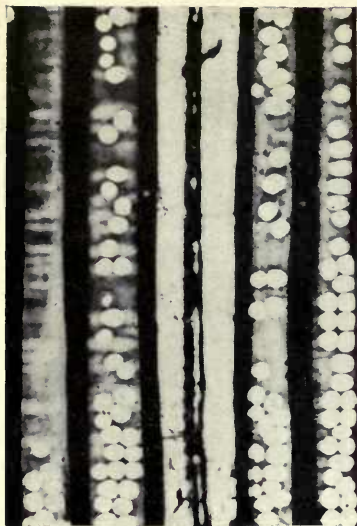


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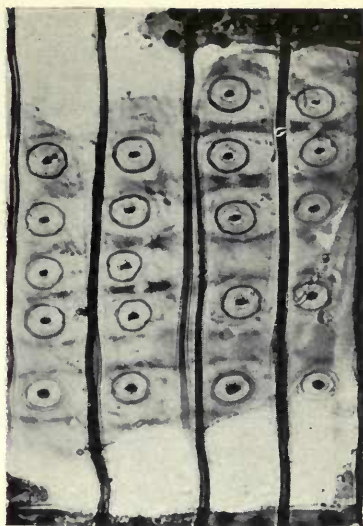


5.

PLATE I



6.



7.

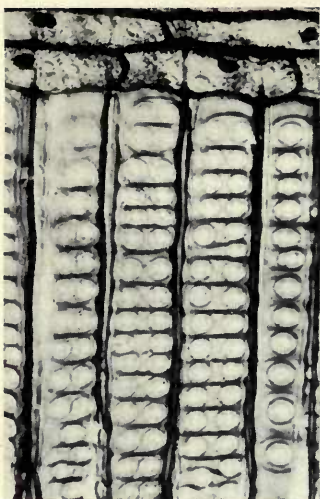


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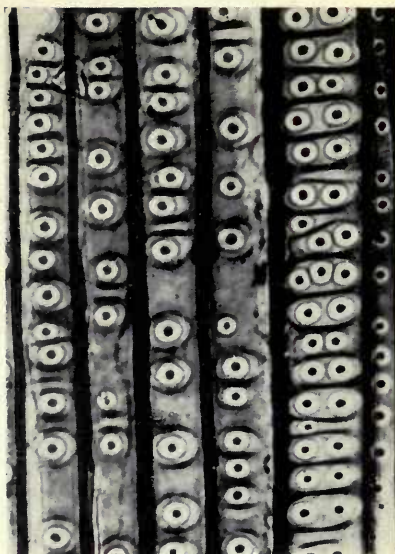


9.

PLATE II



10.



11.



12.

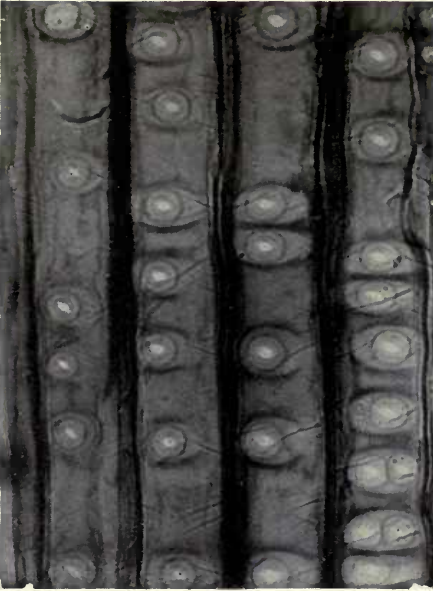


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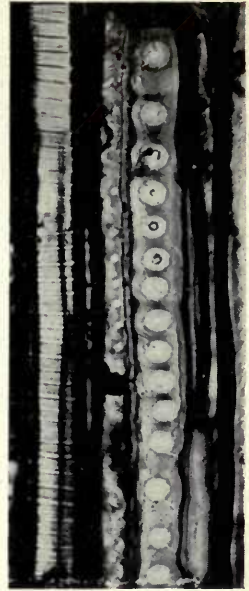


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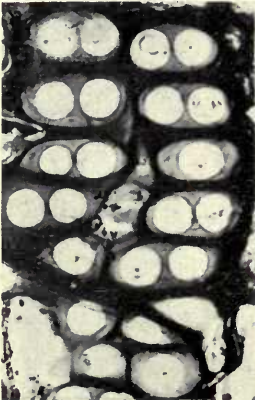
PLATE III



15.



16.



17.

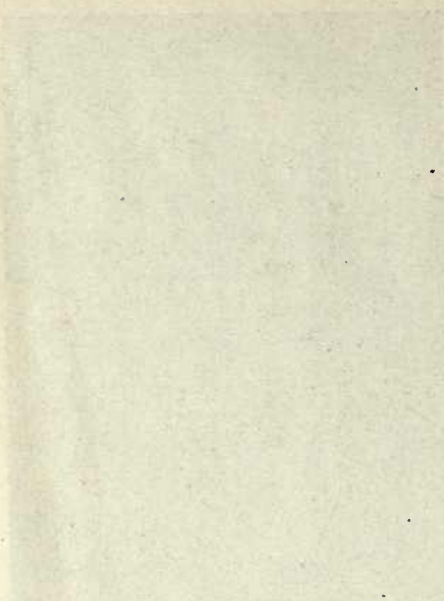


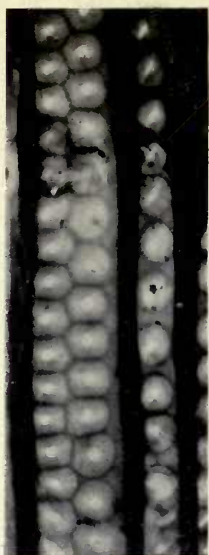
18.



19.

PLATE IV





20.



21.



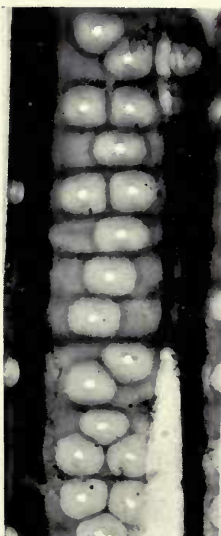
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23.



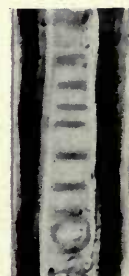
24.



25.

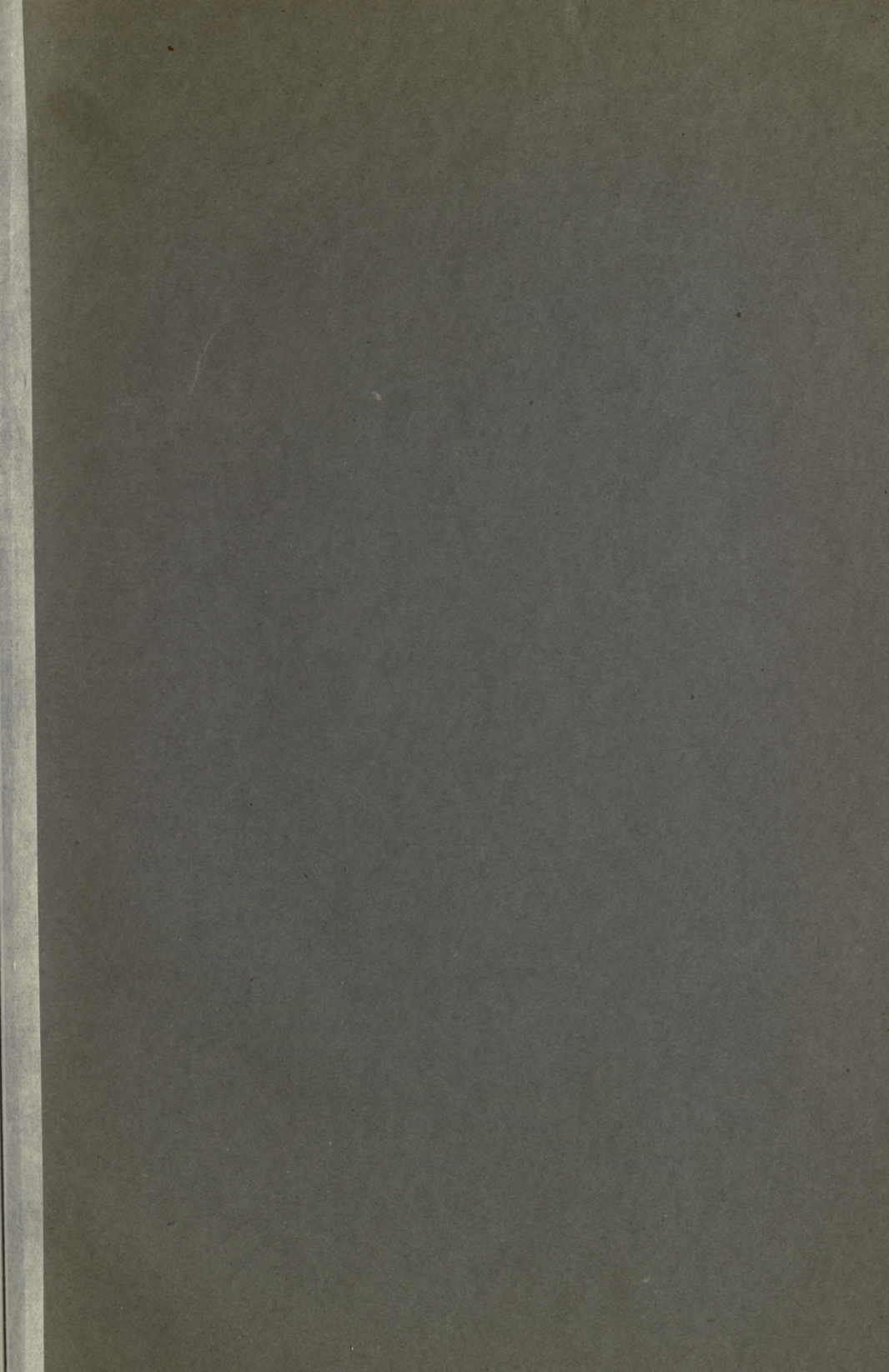


26.



27.

PLATE V



Bot
S

Author Sifton, Harold Boyd

Title Some characters of Xylem tissue in Cycads.

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